

SEXUAL DIMORPHISM IN MOUTHPARTS OF *BLEPHARONEURA* LOEW (DIPTERA: TEPHRITIDAE)

MARTY CONDON, ANN TRUELOVE, AND LYNN MATHEW

(MC), Department of Biology, Cornell College, 600 First Street West, Mount Vernon, IA 52314, U.S.A.; (AT), Department of Biological Sciences, University of Maryland Baltimore County, Catonsville, MD 21228-5398, U.S.A.; (LM), 114 Bagatelle Road, Dix Hills, NY 11746, U.S.A.

Abstract.—Adults of *Blepharoneura manchesteri* Condon and Norrbom (Tephritidae), which rasp and feed upon living plant tissues, are sexually dimorphic in number and distribution of robust blade-like pseudotracheal ring tips (= blades). Both sexes have similar numbers of pseudotracheae, but labella of females have more than twice as many blades as males. Such sexual dimorphism in labellar rasping surface may be associated with higher nutritional requirements of females. Although sex differences in nutritional requirements have been reported for other tephritid fruit flies, ours is the first report of sexual dimorphism in pseudotracheal characters.

Key Words: labella, phytophagy, fruit flies, Cucurbitaceae

Adult fruit flies in the genus *Blepharoneura* Loew (Tephritidae) abrade and break plant surfaces and feed on released substances. This behavior, unknown in any other fly, varies among species of *Blepharoneura*. Some species feed on surfaces of young leaves, leaving distinctive patterns of lacy holes, while others feed on the tips of pedicels (following abscission of flowers), or on the surface of fruit, leaving distinctive traces as scars on the fruit surface (Condon and Whalen 1983; Condon and Norrbom 1994). While feeding, the abdomen of the fly becomes swollen with fluid the color of the tissue being rasped. Distinctive morphological characters are associated with this behavior (Driscoll and Condon 1994).

Labella of *Blepharoneura* bear rows of blade-like pseudotracheal ring tips (=blades) in a rasp-like arrangement (Driscoll and Condon 1994). Unlike most flies, *Blepharoneura* have rows of two kinds of labellar pseudotracheal rings and ring tips: rows of

open rings with brush-like tips, which form the channel-like pseudotracheae that deliver liquid to the mouth as in most flies (Elzinga and Broce 1986); and rows of highly modified closed rings with blade-like tips, which are offset from and parallel to the channel-like pseudotracheae. Blade-bearing rings are fused along the length of the blades, suggesting that the modified rings function as braces for blades that rasp surfaces of plants (Driscoll and Condon 1994). These distinctive blades are a synapomorphy of the clade (which includes *Blepharoneura* and two poorly known Old World genera, *Hexaptilon* Hering and *Baryglossa* Bezzi) that may be the most basal clade of the Tephritidae (Condon and Norrbom 1994; Han and McPherson 1994).

As a first step toward understanding the functional significance of labellar blades and associated feeding behaviors, we looked for evidence of sexual dimorphism in mouthparts. If blades are used to obtain secondary

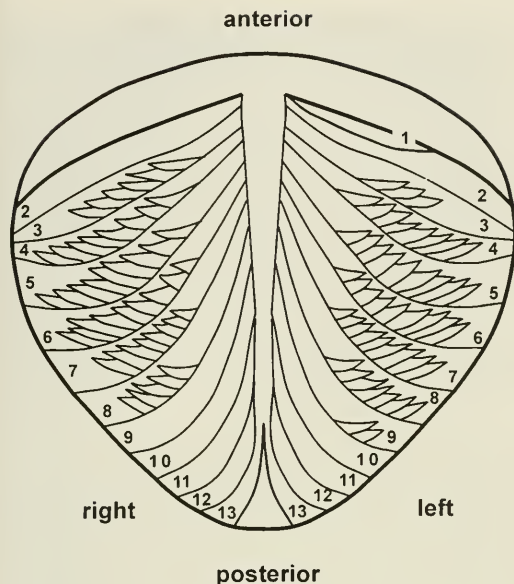


Fig. 1. Arrangement of pseudotracheae and blade-like pseudotracheal ring tips (blades) on the labella of *Blepharoneura* sp. (drawing based on female specimen F3, see Table 1). To emphasize blades, brush-like pseudotracheal ring tips are not shown. Labella are shown in the open position in which they contact surfaces of plants. Pseudotracheae are numbered from anterior to posterior.

compounds used by males in courtship, we expected males to have proportionately more blades than females. Alternatively, if nutrients or other chemicals obtained during adulthood are used in egg production (Tsitsipis 1989; Hendrichs et al. 1993), we expected females to have more blades than males. To test these hypotheses, we examined male and female specimens of *Blepharoneura manchesteri* Condon and Norrbom, a species that feeds on surfaces of fruit of *Gurania spinulosa* Cogn. (Cucurbitaceae) in northern Venezuela.

MATERIALS AND METHODS

Using specimens of *B. manchesteri* reared from seeds of *G. spinulosa* collected in Guatopo National Park in northern Venezuela, we followed slightly modified techniques of Driscoll and Condon (1994) to prepare labella. We soaked heads of specimens in distilled water for 2–3 days, then boiled specimens briefly in dilute solutions

of KOH or NaOH. After boiling specimens in distilled water, we allowed the water to cool to room temperature, and added a few drops of formaldehyde to the cooling water. Once mouthparts were everted, we prepared specimens for SEM using hexamethyldisilazane (HMDS). Dried specimens were sputter coated with 16 nm of gold and examined with a Hitachi 2460-VP scanning electron microscope.

Beginning with the most anterior pseudotracheae, we counted and numbered pseudotracheae on each labellar surface, and counted blades on each pseudotrachea (Fig. 1). We rotated specimens to get accurate counts because mouthparts were not always evenly everted.

RESULTS

Labella of male and female specimens of *B. manchesteri* differ strikingly in the number and distribution of blades (Fig. 2, Tables 1, 2). Despite small sample sizes, we found statistically significant differences between males and females in number of pseudotracheae with blades, number of blades per pseudotrachea, and total number of blades on labella (Table 2). Females had nearly three times as many blades (92–102) as males (31–44), and blades were located along twice as many pseudotracheae. Males and females differed not only in absolute numbers of blades, but also in proportion of pseudotracheae associated with blades: blades were associated with an average of 48% of pseudotracheae in females, and 23% in males (Table 2). Males and females did not differ significantly in total number of pseudotracheae (Table 2).

In both sexes, blades were concentrated among the more anterior pseudotracheae (Fig. 1; Table 1). In males, blades occurred exclusively along anterior pseudotracheae: all posterior pseudotracheae in males were brush-bordered (i.e. bladeless). In females, blades occurred along no more than a third of the posterior pseudotracheae. In both sexes, the posterior

Table 1. Distribution of blades along pseudotracheae of individual specimens of *Blepharoneura manchesteri*. Pseudotracheae are numbered from anterior to posterior (see Fig. 1). A dash indicates absence of a pseudotrachea. R = right labellum. L = left labellum. Specimens are identified by a number preceded by F (female) or M (male). To highlight anterior to posterior asymmetry of blade distribution on labella, **bold type** indicates presence of blades; a line indicates the halfway point, half of the pseudotracheae are above (anterior) to the line, and half are below (posterior) to the line.

Pseudo-trachea	Female Specimens							
	F3		F9		F38		F45	
	L	R	L	R	L	R	L	R
#1	0	—	0	—	0	0	0	—
#2	0	0	0	0	0	0	0	0
#3	3	6	9	0	8	0	0	0
#4	8	8	9	5	10	11	0	7
#5	9	9	8	10	12	10	9	10
#6	9	9	8	11	12	13	11	12
#7	9	8	7	11	8	10	12	8
#8	7	5	4	9	5	6	9	9
#9	2	0	0	7	0	0	8	7
#10	0	0	0	1	0	0	5	0
#11	0	0	0	0	0	0	0	0
#12	0	0	0	0	0	0	0	0
#13	0	0	0	0	—	—	0	0
#14	—	—	0	0	—	—	0	0
#15	—	—	—	—	—	—	0	0
Total	47	45	45	54	55	50	54	53

	Male Specimens							
	M10		M19		M35		M37	
	L	R	L	R	L	R	L	R
#1	0	0	—	0	0	0	—	0
#2	0	0	0	0	0	0	0	0
#3	0	0	0	0	0	0	0	0
#4	0	0	0	0	6	0	0	0
#5	5	2	9	7	8	8	7	4
#6	7	7	8	8	5	7	5	6
#7	6	6	6	6	0	4	4	5
#8	0	0	0	0	0	0	0	0
#9	0	0	0	0	0	0	0	0
#10	0	0	0	0	0	0	0	0
#11	0	0	0	0	0	0	0	0
#12	0	0	0	0	0	0	0	0
#13	0	0	0	0	0	0	0	0
#14	0	0	—	—	—	—	—	—
Total	18	15	23	21	19	19	16	15

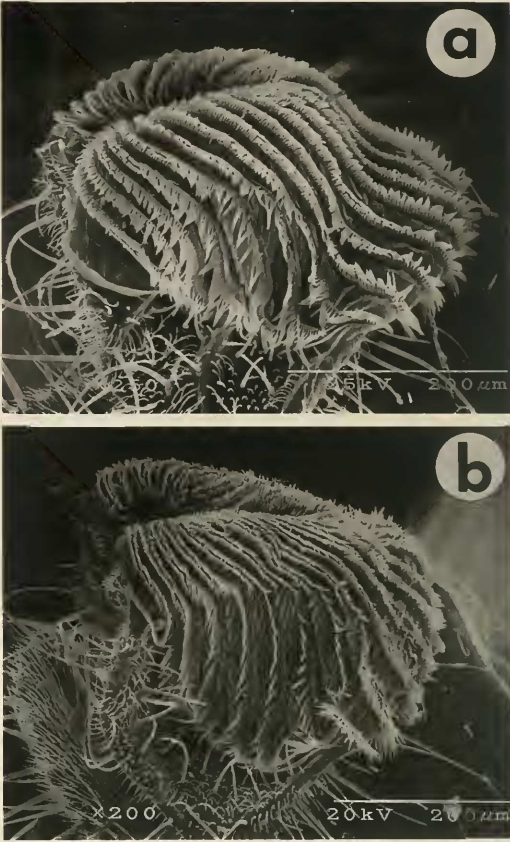


Fig. 2. *Blepharoneura manchesteri*, right labella of male (a, specimen F38) and female (b, specimen M19) specimens (see Table 1). Labella are swollen beyond the “normal” contact position so that all pseudotracheae are visible. Pseudotracheae without blade-like pseudotracheal ring tips (= blades) are bordered on either side by brush-like pseudotracheal ring tips (= brushes). These brush-bordered pseudotracheae are densest posteriorly. Mop-like brushes also occur medially (toward the prestomum) on both sides of pseudotracheae that bear blades. Along the portion of the pseudotrachea where blades occur, brushes are present only along the posterior margin. Posterior and medial arrangements of brushes suggest that brushes function as mops that sop up liquids released by damaged plant tissue.

portion of the labella usually bears at least 50% more brush-bordered (i.e., bladeless) pseudotracheae than the anterior portion of the labella (Table 1).

DISCUSSION

We found significant sexual dimorphism in number and distribution of blades on la-

Table 2. Sexually dimorphic traits of labella of *Blepharoneura manchesteri*. Summary statistics (Mann Whitney U test) for samples described in Table 1: * = $P < .05$, ** = $P < .025$.

Trait	Male N = 4		Female N = 4		P
	Mean	Range	Mean	Range	
Number of pseudotracheae (both labella)	26	25–28	26.3	25–29	NS
Number of pseudotracheae with blades (both labella)	6	6	12.25	11–13	**
% pseudotracheae with blades	23%	21–24%	48%	41–52%	**
Mean number of blades per pseudotrachea with blades	6.1	5.3–7.3	8.3	7.1–9.6	*
Maximum number of blades per pseudotrachea	7.8	7–9	11.25	9–13	*
Total number of blades	36.5	31–44	100.7	92–107	**

bella of *B. manchesteri* (Fig. 2; Tables 1,2). Although both male and female flies rasp plant surfaces, the greater number of blades in females suggests that they are able to cause more damage to a greater surface area of plant tissue than males. The anterior concentration of blades and brushes in both males and females suggest that the mechanism of rasping is similar for males and females (Table 1). The anterior portions of the labella probably make contact with the plant surface first and are moved forward so that tips of blades contact plant tissue. In both sexes, the brush-like pseudotracheal ring tips, which are densest nearest the mouth and along the more posterior pseudotracheae, probably act as mops to sop up fluids released by abraded plant tissues (Fig. 2).

That females have more blades than males is consistent with the hypothesis that the unusual plant-rasping behavior of *Blepharoneura* is associated with different nutritional requirements of males and females. Nutritional requirements of males and females are known to differ in some economically important tephritids (Tsitsipis 1989). In some tephritids, ingestion of nutrients other than carbohydrates during adulthood appears to be necessary for production of eggs, but not spermatzoa (Hendrichs et al. 1991, 1993). Because *Blepharoneura* rasp plants in the Cucurbitaceae, which often contain cucurbitacins—highly bitter compounds (Tallamy and Krischik 1989), rasping behavior also could be as-

sociated with acquisition of secondary compounds that could be used as defenses of larvae or adults.

Are *Blepharoneura* the only tephritid fruit flies with sexually dimorphic labellar surfaces? Despite evidence for sexual differences in nutritional requirements in economically important tephritids, little is known about the functional morphology of their mouthparts. Mediterranean fruit flies (*Ceratitis capitata* (Wiedemann)) have blade-like pseudotracheal ring tips like those of *Blepharoneura*, but the blades are smaller and the blade-bearing pseudotracheal rings are open (like most flies) not highly modified as in *Blepharoneura* (Driscoll and Condon 1994). In contrast to *Blepharoneura* and *Ceratitis*, *Anastrepha*, *Bactrocera*, and *Rhagoletis* lack “blades” and have a scalloped arrangement of pseudotracheal ring tips that may function as filters, not rasps (Elzinga and Broce 1986; Driscoll and Condon 1994). We could not find any studies reporting sexual dimorphism (or lack of) in labellar surfaces of other tephritids. Further study of labellar morphology and feeding mechanisms could lead to improvements in pest control programs that target foraging adults, particularly females (Rössler 1989).

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